

Ephemeromys nov. gen., a primitive prosciurine rodent from the Oligocene of Southern Germany

By WANG BAN-YUE and KURT HEISSIG^{*)}

With 1 figure in the text, 2 plates and 3 tables

Abstract

A new genus and species of the Prosciurinae from the Lower Oligocene fissure filling „Möhren 13“ (Bavaria, Southern Germany) is described as *Ephemeromys hospes* nov. gen., nov. sp. Five specimens from the fissure fillings „Grafenmühle 6 and 7“ from the same region and of similar age are ascribed to it. The new genus, represented by 95 single teeth, four maxillary and four mandibular fragments, is closest to *Prosciurus*, but shows some divergent characters. The discussion concerning the meaning of the different characters in this group leads to the conclusion, that the small group of the Prosciurinae may have separated early from the ancestors of the Allomyinae. Therefore, the separation of these groups on a subfamilial level is retained.

摘 要

本文记述了德国南部巴伐利亚州墨伦十三地奥下渐新统裂隙堆积中的原松鼠亚科的一新属、新种：*Ephemeromys hospes*。另外，还有来自同一时代、同一地区的裂隙堆积，格拉芬米勒六地奥的五块标本也归入了此种中。新种共有九十五个单牙，四个上颌和四个下颌。

新属与原松鼠属最接近，但也有一些分属特征。通过对不同特征的意义讨论，可以得出这样的结论，即：原松鼠亚科可能早就和 Allomyinae 的祖先分开了。因此，这里仍将这两类作亚科级单元予以保留。

^{*)} Frau DR. WANG BAN-YUE, Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, P. O. Box 643, Beijing (28), VR China. – PROF. DR. K. HEISSIG, Bayerische Staatssammlung für Paläontologie und historische Geologie, Richard-Wagner-Straße 10, 8000 München 2.

Kurzfassung

Eine neue Art und Gattung der Prosciurinae aus der unteroligozänen Spaltenfüllung „Möhren 13“ (Bayern, Süddeutschland) wird beschrieben als *Ephemeromys hospes* n. gen., n. sp. Fünf Stücke aus den Spaltenfüllungen „Grafenmühle 6 und 7“ aus dem gleichen Gebiet und von ähnlichem Alter werden dazugestellt. Die neue Gattung, belegt durch 95 Einzelzähne, 4 Ober- und 4 Unterkieferbruchstücke, steht *Prosciurus* am nächsten, zeigt aber einige divergente Merkmale. Die Diskussion der Bedeutung verschiedene Merkmale innerhalb der Gruppe ergibt, daß die kleine Gruppe der Prosciurinae sich wohl schon frühzeitig von den Vorläufern der Allomyinae getrennt hat. Die Trennung dieser Gruppen als Subfamilien wird daher beibehalten.

1. History

Prosciurinae, a subfamily of the Aplodontidae, have been recorded mainly from Northern America. The Oligocene Aplodontidae of Europe, assigned hitherto to the Prosciurinae and the Allomyinae, should be grouped in the latter subfamily, as it is shown in this article.

In America the genus *Prosciurus* was erected by MATTHEW (1903) on the new species *vetustus*. Some years later (1909) he enclosed *Sciurus relictus* COPE 1873 in his new genus. Later the genera *Cedromus* WILSON 1949 and *Pelycomys* GALBREATH 1953 ranged by their authors in different groups, were first assembled by WOOD (1962) in the paramyid subfamily Prosciurinae, erected by WILSON (1949) on *Prosciurus*, together with the Eurasian genus *Plesispermophilus* FILHOL 1883. Already MCGREW (1941), WILSON (1949) and BLACK (1963) had pointed to the relationships of *Prosciurus* and the Aplodontidae. WAHLERT (1974) first took the systematical consequences and included the Prosciuridae (elevated by him on familiar level) in the Aplodontoidea. This view was elaborated by RENSBERGER (1975, as a subfamily of the Aplodontidae) and followed by SUTTON & BLACK (1975) and WOOD (1980). SCHMIDT-KITTLER & VIANEY-LIAUD (1979), studying European Oligocene Aplodontidae, pointed to the strong resemblances of *Plesispermophilus* and the Allomyinae (sensu RENSBERGER) and united the Prosciurinae with this subfamily, excluding on the other hand the four most advanced genera of RENSBERGERS Allomyinae.

The new genus throws a new light on the early history of the Prosciurinae, that may be not only a single side branch of the later lophodont Allomyinae, but a small group of strong bunodont pattern. Therefore the separation on subfamilial level is retained in this paper.

2. Description

Aplodontidae TROUESSART 1897

Prosciurinae WILSON 1949

Ephemeromys hospes gen. et. sp. nov.

Diagnosis of genus and species: A primitive prosciurine, larger in size and more primitive than *Prosciurus*; cheek teeth bunodont; ectoloph of upper cheek teeth absent; paracone large, transverse and protrusive labially; metacone lower, conical; mesostyle distinct, sometimes extended lingually in a crest; protoloph incomplete on P⁴, complete in molars; protoconule distinct; metaloph consisting of more or less separated conules, connected by varying crests with the metacone, the posteroloph or the mesostyle, but never with the protoloph; hypocone generally weak, sometimes indistinct; anterior arm of protocone sometimes with free edge. Anterolophid of P₄ closing trigonid groove; mesostylid large and isolated, sometimes extended labially; mesoconid distinct, equally with occasional labial

extension; entoconid generally separated from posterolophid; hypolophid weak or absent; entoconulid sometimes present.

Holotype: A part of right upper jaw containing M^1-M^3 , BSP 1972 XI 211, Bayer. Staatssammlung für Paläontologie und historische Geologie, München.

Type locality: Fissure filling „Möhren 13“, near Treuchtlingen (Bayern).

Horizon: Suevoium (Lower Oligocene).

Derivatio nominis: Ephemer. (greek) = one day, short duration; hospes (latin) = guest, coming as an immigrant.

2.1. Material

Except a few specimens all material comes from the type locality. Most specimens are in the Bayerische Staatssammlung für Paläontologie und historische Geologie (BSP) in Munich. The specimens from „Möhren 13“ are catalogized with the number 1972 XI 109 and following, the few specimens from „Grafenmühle 6“ under the number 1978 XXIII, from „Grafenmühle 7“ under 1979 XX. Both localities are fissure fillings of approximately the same age as the type locality.

Table 1
Material and measurements of *Ephemeromys* (in mm)

specimen	Inv. Nr. (BSP)	L.	W.	fig.	
l. P^1	1972 XI 214	3.00	2.50		
l. P^4	1972 XI 109	2.49	3.18	pl. 2, fig. 10	
r. P^4	1972 XI 110	2.48	3.29		
l. P^4	1972 XI 111	2.53	3.47		
l. P^4	1972 XI 112	—	—		
r. P^4	1972 XI 113	2.53	3.16		
r. P^4	1972 XI 114	2.33	3.09		
l. P^4	1972 XI 115	—	3.19		
l. P^4	1972 XI 116	—	—		
r. P^4	1972 XI 117	2.44	3.09		
r. P^4	1972 XI 118	2.30	3.16		
r. P^4	1972 XI 119	2.43	3.33		
r. P^4	1972 XI 120	2.62	3.44		
r. P^4	1972 XI 121	—	3.28		
r. P^4	1972 XI 122	2.41	3.17		pl. 2, fig. 9
r. P^4	1972 XI 123	2.49	3.26		
l. P^4	1972 XI 124	2.41	3.15		
l. P^4	1972 XI 125	—	3.50		
r. P^4	1972 XI 126	2.53	3.40		
l. P^4	1972 XI 128	2.50	3.34		
l. P^4	1972 XI 147	2.42	3.33	pl. 2, fig. 8	
l. P^4	1972 XI 206	2.52	3.43		
r. P^4	1972 XI 149	—	—		
l. P^4	1972 XI 216	—	—		
		M^1 2.51	3.36	pl. 1, fig. 9, type	
right maxilla with M^{1-3}	1972 XI 211	M^2 2.59	3.32		
		M^3 2.68	2.98		
l. $M^{1/2}$		1972 XI 127	2.61	3.46	
l. $M^{1/2}$	1972 XI 129	2.60	3.51	pl. 1, fig. 3	
l. $M^{1/2}$	1972 XI 130	2.52	3.46		
r. $M^{1/2}$	1972 XI 131	2.66	3.23		
r. $M^{1/2}$	1972 XI 132	2.58	3.39		

r. M ^{1/2}	1972 XI 133	2.49	3.20	
l. M ^{1/2}	1972 XI 134	2.63	3.39	
l. M ^{1/2}	1972 XI 135	—	—	
r. M ^{1/2}	1972 XI 136	2.70	3.44	
l. M ^{1/2}	1972 XI 137	—	3.26	
r. M ^{1/2}	1972 XI 138	2.53	3.12	
r. M ^{1/2}	1972 XI 139	2.59	3.37	
r. M ^{1/2}	1972 XI 140	2.58	3.38	
r. M ^{1/2}	1972 XI 141	2.78	3.60	
r. M ^{1/2}	1972 XI 142	2.55	3.39	
l. M ^{1/2}	1972 XI 143	2.70	3.47	
l. M ^{1/2}	1972 XI 144	2.55	3.17	pl. 1, fig. 5
l. M ^{1/2}	1972 XI 145	2.48	3.23	
r. M ^{1/2}	1972 XI 146	2.74	3.14	
l. M ^{1/2}	1972 XI 148	—	3.34	
r. M ^{1/2}	1972 XI 150	—	—	
l. M ^{1/2}	1972 XI 151	2.56	3.31	
r. M ^{1/2}	1972 XI 152	2.54	3.20	pl. 1, fig. 7
l. M ^{1/2}	1972 XI 153	2.51	3.30	
l. M ^{1/2}	1972 XI 154	2.47	3.17	
l. M ^{1/2}	1972 XI 155	—	3.37	
r. M ^{1/2}	1972 XI 156	2.54	3.42	
r. M ^{1/2}	1972 XI 157	2.56	—	pl. 1, fig. 8
l. M ^{1/2}	1972 XI 203	—	—	
r. M ^{1/2}	1972 XI 204	—	—	
r. M ^{1/2}	1972 XI 205	—	—	
l. M ^{1/2}	1972 XI 207	2.52	3.26	
l. M ^{1/2}	1972 XI 208	—	—	
r. M ^{1/2}	1972 XI 215	2.60	3.29	
r. M ^{1/2}	1972 XI 310	—	—	
left maxilla with M ²	1972 XI 213	2.63	3.33	
r. M ³	1972 XI 158	2.69	3.01	
r. M ³	1972 XI 159	—	—	
r. M ³	1972 XI 160	2.82	3.08	
r. M ³	1972 XI 161	—	2.93	
r. M ³	1972 XI 162	2.60	2.75	pl. 1, fig. 6
r. M ³	1972 XI 163	2.54	2.77	
r. M ³	1972 XI 164	2.77	3.05	
l. M ³	1972 XI 165	—	2.80	
r. M ³	1972 XI 166	2.62	2.84	
l. M ³	1972 XI 167	2.78	3.07	pl. 1, fig. 4
l. M ³	1972 XI 311	2.53	2.83	
l. M ³	1972 XI 312	2.78	2.93	
l. P ₄	1972 XI 168	2.53	2.48	
l. P ₄	1972 XI 169	—	—	
l. P ₄	1972 XI 170	2.82	2.81	
r. P ₄	1972 XI 171	2.72	2.53	
l. P ₄	1972 XI 172	2.74	2.44	
l. P ₄	1972 XI 173	2.73	2.50	pl. 2, fig. 6
r. P ₄	1972 XI 174	2.69	2.32	pl. 2, fig. 5
r. P ₄	1972 XI 175	2.59	2.53	
l. P ₄	1972 XI 176	2.75	2.47	pl. 2, fig. 4
left mandible with M ₂₋₃	1972 XI 212	M ₂ : 2.86 M ₃ : 2.87	2.81 2.81	pl. 2, fig. 1
l. M _{1/2}	1972 XI 194	—	—	pl. 2, fig. 3
r. M _{1/2}	1972 XI 177	2.83	2.81	pl. 2, fig. 2
l. M _{1/2}	1972 XI 178	—	2.46	

l. M _{1/2}	1972 XI 179	3.10	2.82	
l. M _{1/2}	1972 XI 180	2.93	2.92	
l. M _{1/2}	1972 XI 181	3.05	2.84	
r. M _{1/2}	1972 XI 313	—	2.75	
right mandible with M ₂	1972 XI 209	—	—	
left mandible with M ₃	1972 XI 210	3.09	2.63	
l. M ₃	1972 XI 193	2.94	2.65	
r. M ₃	1972 XI 195	2.95	2.79	
r. M ₃	1972 XI 196	3.28	2.95	
l. M ₃	1972 XI 197	3.12	2.83	
l. M ₃	1972 XI 198	3.11	2.78	
r. M ₃	1972 XI 199	3.11	2.95	
l. M ₃	1972 XI 200	2.73	—	
r. M ₃	1972 XI 201	3.18	2.76	
r. M ₃	1972 XI 202	3.05	2.63	
r. M ₃	1972 XI 212	2.87	2.81	
l. M ₃	1972 XI 314	2.86	2.67	
other localities:				
Grafenmühle 6				
r. M ^{1/2}	1978 XXIII 200	2.42	2.74	pl. 1, fig. 2
P ₄	1978 XXIII 201	3.00	2.75	pl. 2, fig. 7
right maxilla	priv. collection	P ⁴ 2.80	3.15	
	BERGER	M ¹ 2.70	3.25	
	Pleinfeld	M ² 2.65	3.25	
		M ³ 2.80	3.20	
Grafenmühle 7				
r. M ³	1979 XX 8	2.60	2.75	pl. 1, fig. 1
right maxilla	1979 XX 9	M ² —	3.15	
		M ³ (2.3)	—	

2.2. Upper teeth

Maxillary and palatine bones are partially preserved in the upper jaws. The alveolar part of the maxillary looks very thin. The transverse maxilla-palatine suture is situated internal to M². The posterior palatine foramen is lying in the palatine just a little behind the suture.

There is one upper incisor, that may be tentatively ascribed to this species. It is oval in cross section. The enamel on the anterior surface is nearly smooth and shows fine inconstant, divergent rugosities. It is broader than the incisor ascribed by DEHM (1950) to *Paracitellus* and exhibits a simple type of wear. As the only rodent genera of this size in the type locality, *Pseudosciurus* and *Paracitellus* have much narrower incisors, the determination as *Ephemero-mys* seems the only possible in the moment.

P⁴ is triangular in shape, with a much convex external wall. The protocone is the highest and largest among all the cusps and is connected with the anteroloph and the posteroloph respectively. Its anterior arm is slightly protruding between the protoloph and the anteroloph. The large transverse paracone is very characteristic. It protrudes labially beyond all the other external cusps so that the labial wall of the tooth is convex. The small metacone unites with the posteroloph. The conical protoconule does not link up with the paracone but connects mostly only with the protocone by a weak crest, so that the protoloph is incomplete. The metaconule, which is seldom connected with the protocone, varies greatly in size, form, number and in the

degree of its connexion with the metacone (see Table 2). The transverse valley between the protoloph and the metaloph is widening labially. The rather prominent parastyle, which stretches transversely, protrudes slightly anteriorly, but not labially. The distinct mesostyle is separated from the paracone and metacone, and sometimes extends lingually a spur, sometimes possesses even an accessory cingular cusp. There exists no metastyle. The hypocone is indistinct. The anteroloph is short and lower than the posteroloph which possesses occasionally a small cusp. No cingulum is present except 1972 XI 111, in which a weak continuous internal cingulum is clearly seen. Except the specimen 1972 XI 125, which shows a crenulation of metacone and metaconule, the enamel surface is smooth in all P^4 .

$M^{1/2}$: M^1 and M^2 resemble each other and differ from P^4 only slightly. It forms an isosceles triangle with a straight anterior side because the parastyle is not so protrusive anteriorly as in P^4 . The paracone is high, in form of a transverse triangle, but does not protrude labially so prominently as in P^4 . In contrast to P^4 , here the protoloph forms a continuous crest, although developed rather weakly.

It stretches from the internal end of the paracone, passing through the posterior side of the protoconule, just to the protocone. Depending upon the relative position of the protoconule, the protoloph may be straight or curved. As in P^4 metaconule and metaloph are very variable. There is a strong tendency to duplicate the metaconule and its connexion with the metacone. The hypocone, uniting with the protocone is more or less distinct and larger than the protostyle. As in P^4 , the anterior arm of the protocone has sometimes a short free edge. The anteroloph is much more developed than in P^4 , but still a little shorter than the posteroloph. The internal cingulum is absent, the external one seldom developed.

M^3 has the shape of an equilateral triangle and is narrower than $M^{1/2}$. The protoloph is complete, passing through the posterior side of the protoconule or passing by posteriorly to it, then connected to it by a short crest. The metacone being the labial end of the posteroloph is low and indistinct. The very variable (Tab. 4) metaconule is connected in most specimens with the posteroloph. The mesostyle, linking more or less with the metacone, extends internally in a crest, which tends to reach the metaconule. The hypocone is weak or may be absent. Neither a distinct protostyle nor a free anterior arm of the protocone can be seen. The posteroloph is shortened compared to the foregoing teeth.

2.3. Lower teeth

P_4 : It is trapezoid, with a very narrow anterior side because the metaconid is very close to the protoconid. So the trigonid is correspondingly very narrow, enclosing a groove in form of a longitudinal slit. The protoconid is a little lower and smaller than the metaconid but not procumbent. The anterolophid is low or replaced by an anteroconid, which dams the anterior exit of the trigonid. The metalophid is complete, forming an angle. The distinct triangular mesoconid lies just at the middle of the ectolophid which is complete and curved, and extends occasionally an external crest which never contacts the external end of the hypoconid so that the anterior and the posterior depressions are equal to each other and all open externally. The large hypoconid stretches antero-internally. The hypoconulid is distinct, extending occasionally an anterior spur. The conical entoconid is partly separated from the posterolophid. The hypolophid tending to reach the hypoconulid is variable and sometimes absent. The mesostylid is separated from both the mesoconid and the entoconid.

$M_{1/2}$: There is a close resemblance between M_1 and M_2 . The shape is also rhomboid but its anterior side is only a little shorter than the posterior one. Though the trigonid is shorter and narrower than the talonid, it is wider than that of P_4 . The metaconid is situated far forward. The

distance between the metaconid and the protoconid is longer. The anterolophid and the anteroconid are both distinctly developed. The metalophid, being lower than the anteroconid, may be complete or incomplete. The talonid is broader but lower than the trigonid. The hypoconid swells downwards and is larger than the protoconid. The hypoconulid is not so distinct as in P_4 . Sometimes there exists an entoconulid. The hypolophid is varied (see the discussion below). Occasionally a small accessory cusp (metastylid?) appears between the metaconid and the mesostylid. The ectostylid is often present, now and again connects with the mesoconid forming an ectomesolophid of which the external end does not unite with the hypoconid.

M_3 : In form it is similar to $M_{1/2}$, but with shorter external and posterior sides. The trigonid is wider and higher than the talonid, but still very short. The anterolophid is longer than that of $M_{1/2}$. The anteroconid is closer to the protoconid than to the metaconid. The metalophid is incomplete. The base of the hypoconid swells mainly posteriorly. The posterolophid is short. The hypoconulid is indistinct but occasionally with an anterior spur. The conical entoconid is more or less separated from the posterolophid, but may continue in a short hypolophid. There exists neither an ectostylid nor an external crest of the mesoconid.

2.4. Variation

Considerable variation is demonstrated on the following teeth structures: metaloph, metaconule, mesostyle, protoconule and hypocone of the upper cheek teeth and metalophid,

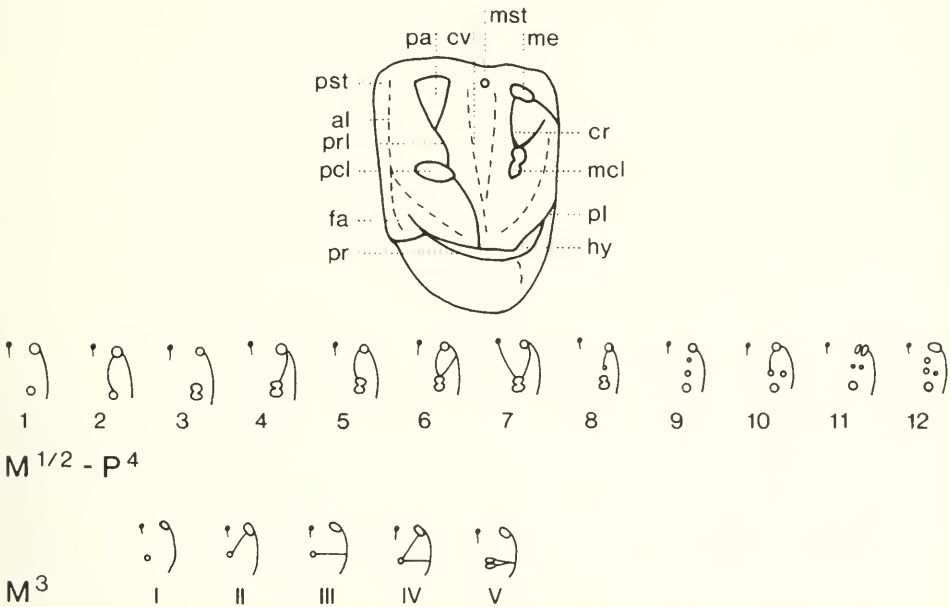


Fig. 1: sketch of an upper $M^{1/2}$ and the types of metacone-metaconule region in $M^{1/2}-P^4$ and M^3 . Abbreviations: al = anteroloph, cr = connecting crests between metaconule and metacone, cv = central valley, fa = free fore arm of protocone, hy = hypocone, mcl = metaconule, me = metacone, mst = mesostyle, pa = paracone, pcl = protoconule, pl = posteroloph, pr = protocone, prl = protoloph, pst = parastyle.

mesoconid and hypolophid etc. of the lower ones. Among them the variations of the metaconule itself and its connexion with other elements, including metaloph, on the upper teeth, and the hypolophid on the lower ones are particularly prominent. So the emphasis of the discussion is here laid on those two structures.

2.4.1. The variation of the metaconule and metaloph on the upper teeth

The metaloph of P^4 is generally not continuous, but the metacone and the metaconule are more or less connected at their bases or by an intermediate cusp. The metaconule may be composed of a single or two cusps. Between the metacone and the metaconule exist one or two intermediate cusps. According to the difference in number of cusps forming the metaloph P^4 may be grouped in 6 types forming a continuous series.

The variation of the metacone-metaconule region is much more complex in $M^{1/2}$ than in P^4 . In addition to the number of cusps involved there occur frequently one or two crests connecting metacone and metaconule. Even these main cusps may be doubled. There may be distinguished a bunodont series with secondary cusps and a more lophodont one with predominant connecting crests. The duplication of metaconule occurs mainly in the lophodont group and is therefore rare in P^4 in which only bunodont types are developed (Tab. 2).

The forming of a double crest or two parallel cuspules between metacone and metaconule is unique in this genus whereas a simple connexion is widespread among Paramyidae and Prosciurinae.

In the M^3 there is less variability, but the mesostyle and the posteroloph are also involved in the connexions with the metaconule. So the 5 types cannot be compared with these of P^4 and $M^{1/2}$ (Tab. 3).

Table 2

Variability of metacone-metaconule region in $M^{1/2}$ and P^4												intermediate			
type number	1	2	3	4	5	6	7	8	9	10	11	12	1-3	3-9	10-11
number of P^4	2	-	14	-	-	-	-	-	2	-	-	-	2	2	1
number of $M^{1/2}$	1	2	2	3	8	9	2	3	-	3	1	1	-	-	-

Table 3

Variability of metacone-metaconule region in M^3					
type number	I	II	III	IV	V
number of teeth	2	3	3	2	3

2.4.2. The variation of the hypolophid in the lower cheek teeth

In the variation of the hypolophid there are involved also other elements as e. g. the entoconulid, the hypoconulid etc. In P_4 the hypolophid may be distinct or indistinct and tends to unite with the hypoconulid. The series from distinct to lacking hypolophid is gradual and allows no grouping in types.

$M_{1/2}$ may be divided into two groups based on the type of hypolophid. In one group it is weak or absent, but a distinct isolated entoconulid is present. In the other one (7 out of 18 $M_{1/2}$) the hypolophid is short but distinct. It meets the hypoconulid only in one specimen.

In M_3 there are 3 types of hypolophid. In most specimens (7 M_3) it is absent or weak. The small entoconulid is connected with the hypoconulid, but not with the entoconid or the hypolophid. In two specimens the base of the entoconid is fusing with the posterolophid but neither hypolophid nor entoconulid are present. One intermediate type exhibits a weak hypolophid and an indistinct entoconulid.

3. Comparison and discussion

The new genus *Ephemeromys* is evidently a primitive aplodontid. It differs from the Paramyidae in the tendency to narrow the main valley of upper molars, the retention of the central position of the protocone and in consequence the less enlarged hypocone. In the lower molars the well developed ectolophid and the prominent mesostylid are advanced features.

From the Sciuridae it is distinguished easily by its extreme bunodont tooth pattern and the diverging tendencies in the connexion of metacone and metaconule as well as in the incipient formation of a hypolophid.

Within the aplodontids it is morphologically in accordance with the Prosciurinae (sensu RENSBERGER 1975) in brachydonty, strong bunodonty, absence of an ectoloph, a rather wide central transverse valley with labial opening, the small mesostyle, the weak development of the free anterior arm of the protocone and the depression opened posterior to the mesoconid.

Within the Prosciurinae the new genus is similar in size to *Cedromus*, which has also a small trigonid and a short hypolophid. But in this genus the protoconule is only a swelling of the protoloph, the metacone and the metaconule are equal in size to the paracone, the mesostyle is connected with the paracone, mesostylid and mesoconid are weak and the entoconid is not separated from the posterolophid. These differences set *Cedromus* farther apart from *Ephemeromys*. If the upper teeth figured by GALBREATH 1953 belong really to *Cedromus* the connexion of the mesostyle to both external main cusps would place this genus nearer to the Allomyinae.

Also from the smaller *Pelycomys* the new genus may be easily distinguished. *Pelycomys* has rounded principal cusps, a larger trigonid, a complete metalophid, a full developed hypolophid, no anteroconid and only one outlet of the talonid basin between entoconid and metaconid. On the other hand the upper teeth are more similar, specially in the isolation of the mesostyle. But this cusp does not extend into the main valley, metaloph and protoloph are more converging.

Spurimus is here not treated as member of the Prosciurinae.

Undoubtedly the new genus is nearest to *Prosciurus* except its size which exceeds far both species of this genus. Both genera agree in having bunodont external cusps in upper cheek teeth, a large mesostyle, a far forward situated metaconid, triangular mesoconid, distinct entoconid and mesostylid, short metalophid, always separated from the ectolophid and a well developed anteroconid. On the other hand there are some differences to one or the other species of *Prosciurus*, that make it necessary to treat both species separately for comparison.

After the revision of STORER (1978) there remain only two species within the genus *Prosciurus*, *P. vetustus* and *P. relictus*, that may represent two evolutionary stages of the same lineage. In *P. relictus*, the more recent one, there are some progressive characters as fusion of protoloph and metaloph before joining the protocone (not all specimens), a large separate hypocone and the prolongation of the hypolophid to contact the ectolophid or the mesoconid. These tendencies are known also from the Allomyinae and may be common tendencies of all Aplodontidae. These characters are not present in *Ephemeromys* as well as in *Prosciurus vetustus*.

Some of the characters separating *Ephemeromys* from *P. vetustus* may be primitive ones: A less marked free fore arm of the protocone, no connexion between protocone and protoconule in P^4 , a trigonid with a complete angled metalophid in all P_4 and even some M_1 and a less developed hypolophid.

On the other hand there are new divergent tendencies in *Ephemeromys*: A double connexion of the metacone with the metaconule, sometimes connexion of metaconule and mesostyle, separation of the protoconule from the protoloph in M^3 . None of these characters are known from any American prosciurine.

Some other differences cannot be decided to be progressive or primitive: In *Ephemeromys* the trigonid groove of P_4 is closed anteriorly whereas it is open in *P. vetustus*. The configuration of

metacone, metaconule and posteroloph region in M_3 is variable, but different in both genera. The paracone is protrusive only in *Ephemeromys*, specially in P^4 .

The question if our new European genus may be related to an Asian stock of prosciurines cannot be solved on the basis of the poor material known so far. Only two well established species may belong to this group: *Prosciurus arboraptus* from the middle Oligocene and *P. lobiculus* from a little higher stratigraphic level. The opinions concerning the systematic position of the latter species are differing. MATTHEW & GRANGER (1923) referred their new species to *Prosciurus* because of its similarity in tooth structure and the protrogomorphous skull. Later on WOOD (1962) believed, that the species should be transferred to *Plesispermophilus*, pointing to a tooth referred to *Plesispermophilus angustidens*, showing in his opinion a pattern representing the initial stages of a trend in the direction to *P. lobiculus*. SHEVYREVA (1976) followed WOODS opinion, while RUSSELL (1972) and KOWALSKI (1974) still argued for the original determination. SCHMIDT-KITTLER & VIANEY-LIAUD (1979) based on a study of good samples of *Plesispermophilus* pointed out that *P. lobiculus* is quite different from *Plesispermophilus* in tooth structure and therefore should be kept in the genus *Prosciurus*.

The Asian prosciurines are indeed quite specialized – and so dissimilar also to *Ephemeromys* – in the longitudinal connexion of protoconule, metaconule and posteroloph and in the poor development of the mesostyle by which they resemble *Prosciurus altidens* from America, in our opinion also differing in essential characters from *Prosciurus*. Even if there are some tendencies in *Ephemeromys* to form longitudinal connexions from the metaconule to the posteroloph in some M^3 or from the protoconule to the anteroloph in two P^4 , there is no crest linking protoconule with metaconule in *Ephemeromys*. Only a small accessory pillar on the backside of the protoconule of two P^4 may be interpreted with doubts as a similar structure.

More important is the fact, that extreme bunodonty and a well developed mesostyle are trends in a direction opposite to that of the Asian species. The Asian species of *Prosciurus* (*P. lobiculus* and *P. arboraptus*), possibly *P. altidens* from North America included, may represent a genus separate from *Prosciurus*, even a separate side branch of the Prosciurinae. If these species will not be found one day to be Cylindrodontids, they may possibly represent an early stage of modern Aplodontidae. Without new and better material the problem cannot be resolved.

4. Conclusions

The ancestor of the Prosciurinae is so far unknown. There is no doubt, that it must be looked for in the big bulk of Paramyidae. The similarities of members of both groups have been discussed by MATTHEW (1910), MILLER & GIDLEY (1918), WILSON (1949) and WAHLERT (1974). WILSON has pointed out, that *Cedromus* comes even nearer to the paramyid structure and narrows so the gap between both groups.

This is also true for *Ephemeromys* nov. gen., but in other characters, so that now there may arise the possibility to compile the plesiomorphic features of these most primitive forms as the hypothetical morphology of the common ancestor: The upper teeth may have had a rather bunodont pattern with only very weak connecting ridges between paracone, protoconule and protocone and without any crest between metaconule and protocone. The mean lochs were tending to one another, narrowing the mean valley and connecting paracone and protoconule at their posterior, metacone and metaconule at their anterior bases – a tendency standing at the beginning of aplodontid evolution. The hypocone should have been less developed as in most Paramyidae. The protocone was elongated with a short free fore arm. There was no ectoloph. The isolated, round or triangular mesostyle may have tended to elongate into the transverse

valley. The paracone was extended labiolingually and compressed in the opposite sense. If there was a tendency to double the metaconule, it may have been in the variation since the paramyid origin.

The lower teeth may have been very near the primitive paramyid structure, but differing not only by the separation of the entoconid from the posterolophid, but also by the first traces of a hypolophid, connecting the entoconid with the hypoconulid. There was no separation of a mesostylid from the posterior metaconid ridge (in this character *Cedromus* is more primitive whereas *Prosciurus* and *Ephemeromys* show the separation as synapomorphy). The trigonid structure was alike *Cedromus* and *Pelycomys*, with a complete metalophid in P₄ and M₁ and a rather long free ending one in M₂ and even M₃. If the anterolophid of P₄ was closed or not cannot be decided.

This hypothetical ancestor of the Prosciurinae may have given rise also to the more modern groups of Aplodontidae. *Prosciurus* and *Ephemeromys* have a few synapomorphous characters, that may constitute the subfamily of Prosciurinae, specially the deep notch between metaconid and mesostylid, lacking in all Allomyinae. It seems therefore necessary to separate Prosciurinae and Allomyinae in contrast to the view of SCHMIDT-KITTLER & VIANEY-LIAUD (1979), which have stressed the similarity of these subfamilies. Nevertheless we agree that *Plesispermophilus* is more similar to the Allomyinae, one of the main reasons of the cited authors to unite the subfamilies. We agree also, that the more modern genera should be excluded from the Allomyinae as SCHMIDT-KITTLER & VIANEY-LIAUD proposed. The position of *Pelycomys* and *Cedromus*, both resembling in the structure of lower molars the Allomyinae, but on a primitive bunodont stage, rests uncertain. The upper teeth ascribed by GALBREATH (1953) to *Cedromus* point also to a relation with the Allomyinae. *Pelycomys* on the other hand has a rounded mesostyle with no tendency to form a selenodont ectoloph.

The primitive Aplodontidae should be therefore rearranged in the following manner:

Family: Aplodontidae

Subfamily: Prosciurinae

Prosciurus MATTHEW 1903

Ephemeromys nov. gen.

? *Pelycomys* GALBREATH 1953

Subfamily: Allomyinae

Allomys MARSH 1877

Haplomys MILLER & GIDLEY 1918

? *Cedromus* WILSON 1949

Plesispermophilus FILHOL 1882

Sciurodon SCHLOSSER 1884

Downsimus MAC DONALD 1970

Some of the few synapomorphies of all Aplodontidae are found also in the genus *Paracitellus* DEHM 1950, considered as a primitive member of Ailuravinae by HEISSIG (1979), specially the separation of the entoconid from the posterolophid, the narrowing of the central valley of upper teeth by protoloph and metaloph and the well developed free fore arm of protocone.

On the other hand an important feature as the hypolophid is missing. Other derived characters are already advanced compared with Prosciurinae as the forming of a low ectoloph and the stronger lophodonty of protoloph. So this group must have split off from the common stock before it reached a definite aplodontid structure. The Ailuravinae may be united with the Aplodontidae only on a superfamilial level.

The same may be true for the Asian „*Prosciurus*“, showing some striking similarities but

combined with a marked hypsodonty and the reduction of the mesostyle. In the moment it is not possible to decide whether the aplodontoid characters of both groups are real synapomorphies or if they have arisen independently.

5. Paleogeographical implications

Ephemeromys is only one of at least 6 genera with American relationships coming to western Europe with the „Grande Coupure“, the great Oligocene immigration. Most of these forms show strong similarities but are not identical with their American relatives:

European immigrant	American relative
<i>Haagella</i>	<i>Colodon</i>
<i>Epiaceratherium</i>	<i>Trigonias</i>
<i>Eomys</i>	div. Eomyidae
„ <i>Shamolagus</i> “ <i>franconicus</i>	<i>Megalagus turgidus</i>
<i>Epoicotherium</i>	<i>Epoicotherium</i>

Two of these groups are obviously of American origin, the Eomyidae and *Epoicotherium*, an edentate. The same seems possible for the Palaeolagidae and *Epiaceratherium*. *Haagella* on the other hand is rather progressive compared with the contemporaneous *Colodon* and may be therefore an earlier offshoot of these American tapirs.

Ephemeromys comes to Europe about the same time as the Prosciurinae arise in North America. The ancestors of both are unknown. So this couple of „orphan“ forms adds no argument for a closer relation of America and Europe in the Oligocene.

Literature cited

- BLACK, C. C. (1965): Fossil mammals from Montana. Part 2. Rodents from the early Oligocene Pipestone Springs local fauna. – Ann. Carnegie Mus., 38: 1–48, 6 pl.; Pittsburgh.
- COPE, E. D. (1873): Third notice of extinct Vertebrata from the Tertiary of plains. – Paleont. Bull., 16: 1–8; Philadelphia.
- FILHOL, H. (1883): Description d'un nouveau genre de Rongeurs provenant des Phosphorites du Quercy. – Bull. Soc. philomat. Paris, (7), 7: 1–2; Paris.
- GALBREATH, E. C. (1953): A contribution to the Tertiary geology and paleontology of northeastern Colorado. – Univ. Kansas Pal. Contrib., Vertebrata, 4: 1–120, fig. 1–26, pl. 1–2; Lawrence.
- HEISSIG, K. (1979): Die frühesten Flughörnchen und primitive Ailuravinae (Rodentia, Mamm.) aus dem süddeutschen Oligozän. – Mitt. Bayer. Staatsslg. Paläont. hist. Geol., 19: 139–169, 7 fig., 6 tab., pl. 20–21; München.
- KOWALSKI, K. (1974): Results of the Polish-Mongolian paleontological expeditions Mongolia. – Paleont. Polonica, 30: 147–178, pl. 43–51, tab. 1–19, 2 fig.; Warszawa.
- MCGREW, P. O. (1941): The Aplodontoidea. – Field Mus. Nat. hist. Geol. Ser., 9: 3–30, 13 fig.; Chicago.
- MATTHEW, W. D. (1903): The fauna of the *Titanotherium* beds at Pipestone Springs, Montana. – Bull. Amer. Mus. Nat. Hist., 19: 197–226, fig. 1–19; New York.
- RENSBERGER, J.-M. (1975): *Haplomys* and its bearing on the origin of the Aplodontoid Rodents. – Journ. Mammalogy, 56 (1): 1–14, 5 fig., Washington.
- RUSSELL, L. S. (1972): Tertiary mammals of Saskatchewan III! The Oligocene fauna, non-ungulate orders. – Life. sci. contr. Roy. Ontario Mus., 84: 1–63, pl. 1–17; Toronto.
- SCHMIDT-KITTLER, N. & VIANEY-LIAUD, M. (1979): Evolution des Aplodontidae Européens. – Palaeovertebrata, 9 (2): 33–82, 19 fig., pl. 1–4; Montpellier.

- SETOGUCHI, T. (1978): Paleontology and geology of the Badwater Creek area, central Wyoming 16. The Cedar Rigde local fauna (late Oligocene). – Bull. Carnegie Mus. nat. hist., 9: 1–61, fig. 1–32, tab. 1–4, append. A–D; Pittsburgh.
- SHEVYREVA, N. S. (1976): Paleogene Rodents of Asia (Fam. Paramyidae, Sciuravidae, Ischyromyidae, Cylindrodontidae). – Trudy Pal. Inst. Ak. Sci. USSR, 157: 1–112, 19 fig., pl. 1–14; Moscow.
- STORER, J. E. (1978): Rodents of the Calf Creek local fauna. – Nat. hist. Contrib., 1: 1–54, 10 fig.; Regina.
- SUTTON, J. F. & BLACK, C. C. (1975): Paleontology of the earliest Oligocene deposits in Jackson Hole, Wyoming 1. Rodents exclusive of the family Eomyidae. – Ann. Carnegie Mus., 45: 299–315, 30 fig., 4 tab.; Pittsburgh.
- WAHLERT, J. M. (1974): The cranial foramina of Protrogomorphous Rodents ... – Bull. Mus. Comp. Zool. Harvard Univ., 146 (8): 363–410, 13 fig.; Cambridge.
- WILSON, R. W. (1949): Early Tertiary Rodents of North America. – Publ. Carnegie Inst., 584: 67–164, 13 fig.; Washington.
- WOOD, A. E. (1962): The early Tertiary rodents of the family Paramyidae. – Trans. Amer. Phil. Soc., n. s., 52: 1–261, 91 fig., 70 tab.; Philadelphia.
- WOOD, A. E. (1980): The Oligocene rodents of North America. – Trans. Amer. Phil. Soc., 70 (5): 1–68, 1 tab.; Philadelphia.

Plate 1

Ephemeromys hospes nov. gen., nov. sp.

1. M³ r., Grafenmühle 7, BSP 1979 XX 8 (with maxilla fragment)
 2. M^{1/2} r., Grafenmühle 6, BSP 1978 XXIII 200
 - 3–9 from Möhren 13
 3. M^{1/2} l., BSP 1972 XI 129
 4. M³ l., BSP 1972 XI 167
 5. M^{1/2} l., BSP 1972 XI 144
 6. M³ r., BSP 1972 XI 162
 7. M^{1/2} r., BSP 1972 XI 152
 8. M^{1/2} r., BSP 1972 XI 157
 9. maxilla fragment with M¹–M³ r., holotype, BSP 1972 XI 211
- all specimens in occlusal view, enlarged 12:1

Plate 2

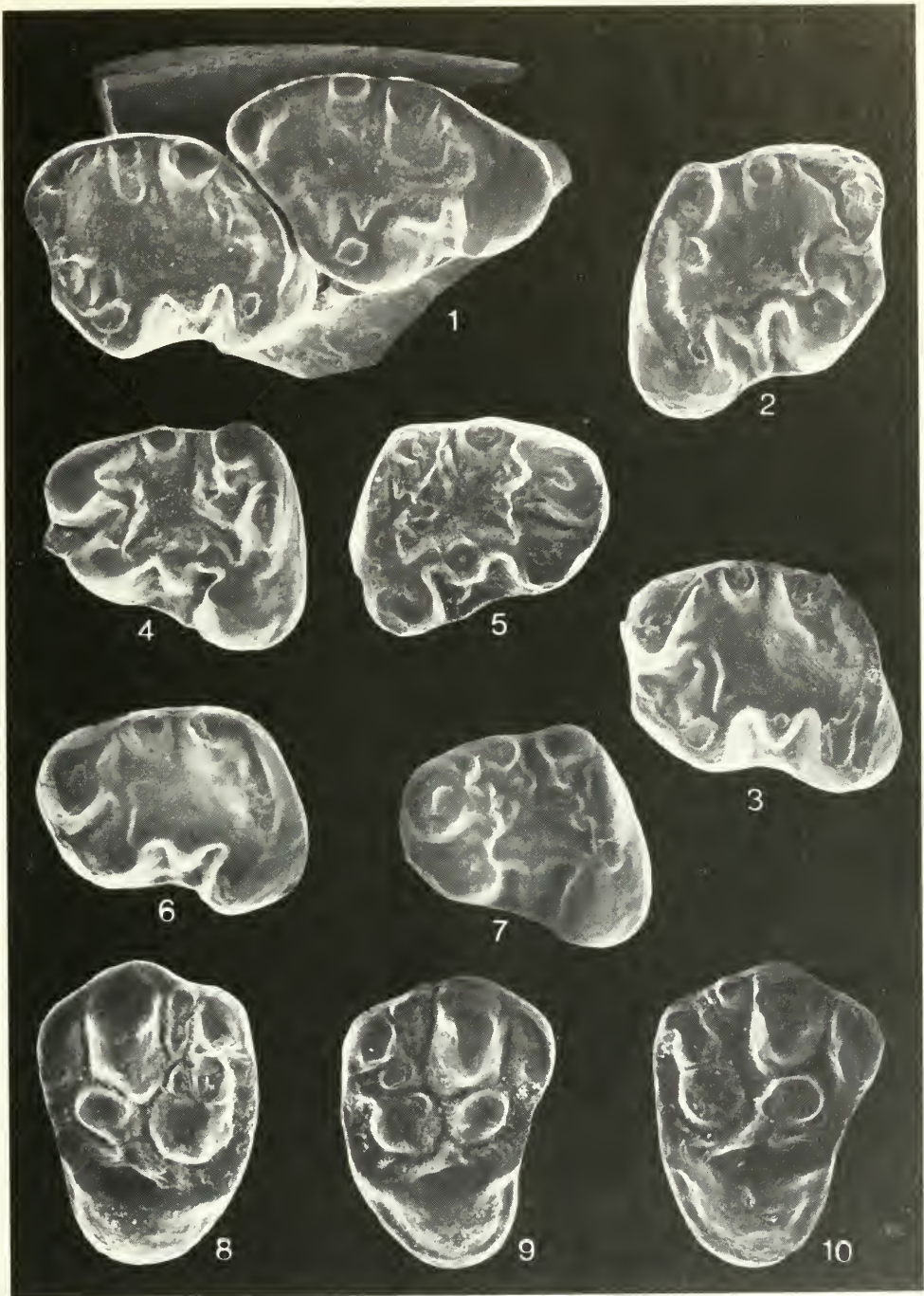
Ephemeromys hospes nov. gen., nov. sp.

- all specimens except fig. 7 from Möhren 13
1. mandible fragment with M₂–M₃ l., BSP 1972 XI 212
 2. M_{1/2} r., BSP 1972 XI 177
 3. M_{1/2} l., BSP 1972 XI 194
 4. P₄ l., BSP 1972 XI 176
 5. P₄ r., BSP 1972 XI 175
 6. P₄ l., BSP 1972 XI 173
 7. P₄ l., Grafenmühle 6, BSP 1978 XXIII 201
 8. P⁴ l., BSP 1972 XI 147
 9. P⁴ r., BSP 1972 XI 122
 10. P⁴ r., BSP 1972 XI 110
- all specimens in occlusal view, enlarged 12:1



WANG BAN-YUE & HEISSIG, K.: *Ephemeronmys* nov. gen.

Plate 1



WANG BAN-YUE & HEISSIG, K.: *Epbemeromys* nov. gen.

Plate 2